THE STRATIGRAPHIC OCCURRENCE OF EARLY LAND PLANTS

by H. P. BANKS

ABSTRACT. Determination of the age of the first land plants depends on sequences established for marine animals and possibly plant spores. *Cooksonia* in the Downtonian of Wales is currently the oldest proven vascular plant macrofossil. Similar appearing plants are found in comparable deposits in Czechoslovakia, U.S.S.R. (Podolia), and the U.S.A. (New York). The vascular nature of older macrofossils is unproven. The considerable evidence of older spores could be interpreted to mean that the separate characters of vascular plants evolved independently. Gedinnian and Lower Siegenian vascular plants differ little from Silurian ones but mid-Siegenian saw the beginning of a marked increase in kinds of vascular plants.

NECESSARILY a report on Silurian-Devonian plant macrofossils must be transitory in nature. This results from repeated revisions of stratigraphic boundaries for geological or palaeontological reasons, the latter being the result of taxonomic revisions of organisms used in the correlation of strata. Equally important are additions to the list of macrofossils as the early strata and their flora are analysed more often and more carefully.

The sparse occurrence of good macrofossils of this age and the manner of their occurrence in rock strata make paleobotanists dependent upon colleagues who study environments of deposition and the stratigraphic occurrence of plant spores, graptolites, conodonts, ostracods, brachiopods or fish. When these fossils are found intermingled with the plants in strata deposited under marine conditions, the strata can be dated with some accuracy. But plants are more numerous and preserved in greater detail in beds laid down under continental conditions, in which many of the stratigraphically important animal fossils are lacking and precise dating and correlation are more difficult. Unless the stratigraphy of the plant-bearing horizons is worked out successfully by a variety of approaches and at many localities, there is little object in generating much enthusiasm about such problems as the first appearance of vascular plants. It is, however, the painstaking acquisition of anatomical and structural details that will characterize any significant advances in the study of early plant macro-fossils. These guidelines account for both the inclusions and the obvious omissions in the following discussion.

The work of Lang (1937), who erected the genus *Cooksonia* for fossil plants found throughout the Downtonian strata of Wales, still stands as the foundation record of early vascular plants. He demonstrated unequivocally the presence of tracheids in stems, and of trilete cutinized spores. The slender (0·25–1·5 mm) stems bore no appendages, forked dichotomously, and bore terminal, globose (1·0 mm long by 2·0 mm wide) sporangia. Basal axes are unknown but *Cooksonia* presumably reached a height of at least several inches.

Since *Cooksonia* is as simple a vascular plant as one can imagine, its age is of immediate concern. The Downtonian has variously been treated as uppermost Silurian or lowermost Devonian. A long series of discussions on the position of the Silurian-Devonian boundary culminated in an informal agreement that the base of the

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TABLE 1. Suggested equivalencies of some units of Silurian–Devonian, some graptolite zones, and occurrences of dispersed spores. Numbers in Stage column indicate time of beginning in millions of years (Devonian from Harland *et al.* 1964). Table compiled from Berry 1970, Chaloner 1970, Martinsson 1969, Richardson and Lister 1969, Banks (in press).

PERIOD	Stage	Bohemia	Graptolite Zone	Spores	U.S.A.	Britain	Podolia
LOWER DEVONIAN	Emsian 374	Pragian	yukonensis ↕			? Rhynie Chert ?	
	Siegenian 390	Lochkovian		11 genera		Senni Beds	Dnestr Ivane
	Gedinnian 395		uniformis	20 spp.		Cairnconnan Group Carmyllie Group	Czortkov Borschov
SILURIAN	Přidolian 405	Přidolian Budňany	angustidens ↕ ultimus	8 genera 24 spp.	Cayugan Series	? Downtonian L.B.B.	Skala
	Ludlovian 415	Kopaninian	fecundus ↕ nilssoni ludensis	6 genera 15 spp.		Ludlovian	
	Wenlockian 425	Motolian	lundgreni ↕ murchisoni	4 genera 15 spp.		Wenlockian	
	Llandoverian 435	Zelkovician	crenulatus ↕ acuminatus	1 genus 2 spp.		Llandoverian	

Monograptus uniformis zone of graptolites shall be taken as the base of the Devonian Period (e.g. Bouček, Horný and Chlupáč 1968, Berdan *et al.* 1969, Martinsson 1969, Berry 1970). This agreement, if formalized, by no means solves all the problems involved but at least it may permit certain international correlations and enable students of plant macrofossils to use their data more intelligently. One of the correlations equates the Welsh Downtonian with the Pridoli beds of Czechoslovakia (Table 1). If this equivalence is accepted, Lang's *Cooksonia* is Silurian rather than Devonian in age. It becomes at once the oldest proven vascular plant and the simplest one morphologically.

In 1962 Obrhel described specimens attributable to *Cooksonia* from the Pridoli strata of the Silurian in Czechoslovakia (Table 1). At the time they seemed older than Lang's collections because the Downtonian was then still regarded as Devonian in age. Now the two occurrences may be nearly contemporaneous. Obrhel's plants consisted only of compressions from which no evidence of their vascular nature could be obtained. I was able to study them in the National Museum of Prague through the courtesy of Dr. V. Zazvorka, Director of the Department of Palaeontology. They seemed very probably to be vascular plants.

Ishchenko (1969) and Banks (in press) have reported two new occurrences of *Cooksonia* in strata of about the same age. The former came from the Upper Rashkov beds of the Skala Formation in Podolia and the latter (Pl. 65, figs. 1–2) from the Bertie Formation of the Cayugan Series in central New York State. In neither case is there proof that the specimens are vascular plants yet both suggest this strongly. The age of the Bertie Formation is based on occurrences of conodonts and brachiopods (Berdan *et al.* 1969), but it is clear that all possible lines of evidence must be pursued. Conodonts, brachiopods and ostracods are currently in use but it is clear that plant spores will soon begin to play a larger role, especially in continental deposits (e.g. Richardson and Lister 1969).

Edwards (1970*b*) has described fertile specimens of *Steganotheca*, another vascular plant, from the Lower Downtonian of Wales and similar sterile axes from the immediately underlying Ludlovian strata.

It must be emphasized that three Silurian occurrences (Table 2) of *Cooksonia* and the *Rhynia*, the ?*Taeniocrada* and the cf. *Steganotheca* all lack proof of their vascular nature. Their credibility is dependent on close resemblance to Lang's proven specimens of Downtonian age, or to younger fossils.

The assumption that macrofossils of simple vascular plants first appeared in rocks of Late Silurian age requires support from collateral evidence.

PLANT SPORES

Morphological evolution. Chaloner (1967) drew together in graphic form the then available data on isolated, cutinized spores regarded as originating from vascular plants. His analysis showed a steady increase in the number and kind of spores from Silurian throughout Devonian strata. One of the most straightforward changes was increase in diameter. This related directly to a major evolutionary event among vascular plants, the evolution of seeds. Vascular plants at first produced one kind of sporangium containing one kind of spore and were homosporous. Heterospory and then the seed habit were believed to follow in that order. Fossils bearing attached sporangia actually containing larger megaspores and others with smaller microspores first appear in Frasnian rocks. But Chaloner's analysis of dispersed spores showed some exceeding the arbitrary diameter of 200 μm by Emsian time. On the assumption that spores over 200 μm in diameter may be megaspores, the occurrence of some spores of that size in late Lower and Middle Devonian implies the existence of heterospory many years before it can be demonstrated objectively in early Upper Devonian. It still remains to be learned whether any Middle Devonian plants actually bore two sizes of spores and were truly

TABLE 2. Fossils indicative of vascular plants in Silurian and Early Devonian time. Vascular tissue has been proven only for *Cooksonia* from Wales and *Zosterophyllum* from Scotland.

EARLY LOWER DEVONIAN	Gedinnian	*Cooksonia caledonica* (Scotland; Edwards 1970*b*)
		C. downtonensis (Obrhel 1968)
		Zosterophyllum myretonianum (Scotland; Lele and Walton 1961)
		Taeniocrada (?) *spitsbergensis*, *Hostimella* sp., *Zosterophyllum* sp. (Spitsbergen; Høeg 1942)
SILURIAN	Downtonian	*Cooksonia* (Wales, Bohemia, Podolia, New York State)
		Steganotheca striata (Wales; Edwards 1970*b*)
		Rhynia major (Podolia; Ishchenko 1969)
		?*Taeniocrada* sp. (Bohemia; Obrhel 1962)
		8 genera, 24 spp. of spores (Richardson and Lister 1969)
	Ludlovian	cf. *Steganotheca* (Wales; Edwards 1970b)
		6 genera, 15 spp. of spores (Wales; Richardson and Lister 1969)
	Wenlockian	4 genera, 8 spp. of spores (Wales; Richardson and Lister 1969)
	Llandoverian	1 genus, 2 spp. of spores (Libya; Hoffmeister, see Richardson and Lister 1969)

heterosporous or whether they showed simply some kind of incipient heterospory. Nevertheless the hypothesis that evolution proceeded from homospory to heterospory to the seed habit now rests on a much more continuous succession of evidence than previously. The discovery of a Famennian seed (Pettitt and Beck 1968) was an event that had long been expected and awaited.

Chaloner (1963), Richardson (1964), Mortimer (1967), Chaloner and Streel (1968) provide valuable additional evidence that spores were at first few and morphologically simple, and gradually increased in number and diversity.

Stratigraphic significance. Assuming that early spores were significant morphologically, what of their stratigraphic value? Richardson and Lister (1969) studied Silurian-Lower Devonian spores from a number of localities in the Welsh Borderland and South Wales. They accept the spores described by Hoffmeister from the Late Llandovery in Libya as the earliest record of possible vascular plants and record a steady increase in variety from the Wenlock, Ludlow, and Downtonian of Wales. Their figures for number of taxa in each Stage are given in Table 1. The increase in the Downtonian is especially sharp. Despite the lack of absolute proof that all these Silurian cutinized spores with triradiate marks were produced by vascular plants, they do provide the basis for a stratigraphic column against which spores from strata whose age is uncertain could be matched.

Time of appearance. The further question arises: why should spores appear in the record earlier than the plants from which they should have originated? Referring to the sedimentological and paleoenvironmental studies of Allen and Tarlo (1963) in the Welsh Borderland, Richardson and Lister (1969) note that their older spores came from off-shore, marine strata, younger ones from near shore deposits, and the youngest from continental beds. Assuming that all the spores belonged to vascular plants, this could mean that there were vascular plants on the land in Wenlockian and Ludlovian time in an unknown abundance and that they were rarely or never preserved as fossils in the marine strata. Despite the discrepancy in time of appearance of the spores and the macrofossils, the evolutionary value of the spores seems assured. The evolutionary advance in spore morphology that is evident in successively younger horizons is independent of both the abundance of spores and their position relative to the Devonian shoreline (Richardson and Lister 1969). Another possible explanation of the earlier appearance of spores is given below.

Affinity of the spores. It is of importance that the number of spores found *in situ* in sporangia attached to vascular plant fossils be increased. This is essential to demonstrate that we continue to deal with valid evidence. Among others, I attempted a preliminary list of spores that have been reported both dispersed and in place (Banks 1968). Potonié (1970) has recently completed an extensive systematic study of plants and their associated spores. Occasionally the spores found within sporangia are too poorly preserved or too difficult to extract to assign to one of the taxa erected for dispersed spores (Edwards 1970*a*). There may also be a serious question in identification caused by the stage in maturation of the spores that are found in place. One does not really know how many whole plants are represented by the many names applied to dispersed spores because we know too little about their ontogenetic development before dispersal and about the variation to be found within a single sporangium. Progress is slow but what there is indicates that at least the spores from the Downtonian onwards do represent vascular plants.

Thus it is reasonable, on the evidence from spores, to conclude that vascular plants evolved during the Silurian Period and that evolutionary change marked their early appearances just as it does today. It is also reasonable to conclude that we may find vascular plant macrofossils earlier than uppermost Silurian strata. This would require one of two activities. Either marine strata must be examined more carefully for the occasional preserved macrofossil or we must locate more, and study carefully, on-shore deposits of Early Silurian age in the belief that they might contain macrofossils. Is there another possibility?

TIME OF EVOLUTION OF BIOCHARACTERS

All paleobotanical evidence indicates that some biocharacters associated with vascular plants evolved earlier than others. I mentioned above that homospory preceded heterospory and the seed habit in time of appearance in the fossil record. The papers by Chaloner (1970), Beck (1970), Pettitt (1970), and Banks (1970), include many more examples. It seems reasonable to conclude that the basic characters regularly associated with vascular plants could have evolved independently in precursor groups. The usual requirements for a certain identification of a vascular plant are: the differentiated tissues xylem and epidermis plus stomates, and cutinized spores borne in a tetrad following meiosis and marked by a trilete ridge when separated. These requirements are reasonable once the course of evolution had reached the stage where all were present in an organism. But what about the organisms that are presumed to have evolved from the algal ancestors yet still possessed only some of the biocharacters required of a vascular plant? On this subject one can only speculate but one good example is already available.

Schopf *et al.* (1966) erected the genus *Eohostimella* for small, cylindrical axes of Late Llandovery age that they interpreted as erect, land plants. The only cells preserved were thick-walled cells located inside the periphery of the stems in the position of the cortex. Vascular tissue, if ever present, was not preserved. The authors speculated that these slender plants could have maintained an erect habit on the basis of the cortical thickening regardless of the presence of xylem tissue. Incidentally, several early vascular plants are characterized by thick-walled cells in the cortex (Banks and Davis 1969, Edwards 1969, 1970*a*, Hueber and Banks 1967). *Eohostimella* then could have been an organism in which some but not all of the characters of a vascular plant had evolved. The independent evolution of biocharacters could account for a plant with this structure. Did it possess also trilete spores? Obviously we do not know because no sporangia were found. *Eohostimella* also suggests that occasional reports by geologists of the occurrence of unprepossessing axes amid plant-like debris in Early Silurian strata should be investigated fully rather than passed up as I have done in the past. If Schopf *et al.* are correct in their interpretation of *Eohostimella*, the lowlands of Llandovery time may have been occupied by plants that cannot be called vascular plants but which had begun to evolve in that direction.

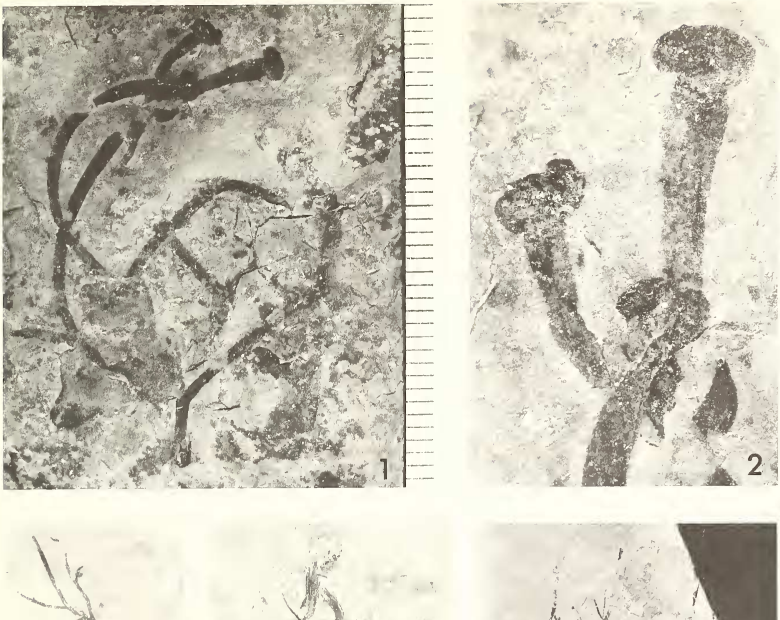
On the same interpretation of the independent origin of biocharacters, it would be reasonable to speculate that some or all of the triradiate spores found in Llandoverian, Wenlockian, and Ludlovian strata could have evolved in various kinds of early plants independently of the rest of the characters of vascular plants. Such a course of events would not affect the stratigraphic value of the spores nor would it preclude the occurrence of the same kind of spore at a later date in a true vascular plant. It would mean only that at a given time in, say, the Wenlockian the suite of characters of vascular plants had not yet been 'assembled' (evolved) in a single organism acceptable to all workers as a good vascular plant.

EXPLANATION OF PLATE 65

Figs. 1–2. *Cooksonia* sp. 1, Group of axes from Fiddlers Green member of Bertie Fm, Cayugan Series, Late Silurian of central New York State; ×2·5. Scale on right is in mm. 2, Enlargement of distal portion of two axes to show short, broad sporangia; ×6·5.

Figs. 3–4. Possible vascular plant fossils from same locality and horizon as *Cooksonia* sp. in Figs. 1–2. 3, ×1. 4, ×1·5.

Fig. 5. Possible alga from same locality and horizon as the plants in Figs. 1–4; ×0·6.



BANKS, Late Silurian land plants

CONCOMITANT EVOLUTION

(*a*) Nematophytales. In Wenlockian strata there appear strange organisms assigned to the genus *Prototaxites*. Some specimens in Late Silurian or Early Devonian reached the size of tree trunks and indeed Dawson originally believed them to be ancient precursors of the modern gymnosperm *Taxus*. However their body consists solely of masses of cylindrical tubes, some larger, some smaller. Many investigators have placed *Prototaxites* among the brown algae (e.g. Pia, in Hirmer 1927). Other workers are inclined to regard the nematophytes as plants that reached a cryptogamic level of evolution without evolving vascular tissue.

Lang (1937) in his careful analysis of the plants of the Welsh Downtonian described another organism as *Nematothallus*. It consisted of flattened carbonized fragments, quite nondescript, on the rock. From these he macerated out a pseudocellular cuticle, firm, probably cutinized spores with a trilete mark, and a central mass of both large and small cylindrical tubes like those of *Prototaxites*. Spores were simply dispersed among the tubes. The smaller tubes were more densely aggregated near the periphery of the specimen, the larger occurring nearer the centre. Some thin-walled tubes showed annular internal thickenings of the wall such as one associates with primary xylem cells of vascular plants. Lang noted that he had seen but not described *Nematothallus* in Ludlovian strata also. He considered the possibility that *Nematothallus* might have formed the terminal portions of the *Prototaxites* plant.

Along with *Prototaxites* and *Nematothallus* Lang collected *Pachytheca*, a free-rolling algal mass or colony, and *Parka* a strange organism of cellular construction, and with cutinized spores. *Pachytheca* might have inhabited fresh or brackish water and *Parka* might have lived on mud or soil and produced airborne spores. In the Downtonian all of these genera occurred alongside the undoubted vascular plant *Cooksonia*.

Lang argued that this assemblage of fossils represented a land flora. He noted that in the Ludlow Bone Bed at the base of the Downtonian the plants were associated with marine invertebrates. In successively younger strata the number of marine forms decreased until he found the same assemblage of plants with no sign of marine invertebrates. In the Carmyllie and Cairnconnan beds of Scotland a similar flora was associated with fish, eurypterids, and myriapods. Lang regarded the uniformity of the flora throughout its range and its close association with continental organisms in the younger strata as clear evidence that the plants occupied terrestrial and not marine habitats. The early occurrence of the flora in marine strata, meant only that, as often happens to land plants, they were washed into the marine environment prior to fossilization.

(*b*) Charophyta. A strange group of green algae characterized by whorled branching and by oogonia surrounded by spirally twisted cells can also be regarded as algae that invaded the land, inhabiting only fresh water. Croft (1952) reported *Trochiliscus* from the Late Downtonian of Podolia. The specimens appear unquestionably to be oospores of a charophyte and they may be the oldest representatives of the group.

Croft (1952) detailed all the arguments for considering charophytes to be land plants. These include their occurrence as fossils in continental strata lacking any marine animals, and the rarity of their occurrence in littoral marine environments into which they may have been washed from the land. Additionally the oospores were surrounded by a resistant membrane and the spore itself may have contained the reserve food starch.

These facts are in accord with the notion that land plants frequently must survive desiccation. To Croft the evidence indicated that this group of algae was becoming adapted to life on the land more or less simultaneously with the appearance of vascular plants on the land.

Thus Nematophytales and charophytes contribute to the hypothesis that during Silurian time the evolution of biocharacters was resulting in organisms capable of life on land. The nematophytes became extinct during Devonian, the charophytes have persisted to the present. The former perhaps failed in competition with plants whose supporting, conducting, reproductive and other systems were better adapted, but they clearly indicate a tendency toward elongate cells enclosed by an outer cylinder of smaller, differentiated cells. They also help make plausible the hypothesis that some plants of Silurian age may have possessed some but not all the attributes of vascular plants.

ECOLOGY OF DOWNTONIAN PLANTS INFERRED FROM PALAEOENVIRONMENTAL STUDIES

(*a*) Wales. According to Allen and Tarlo (1963) the Ludlow series was deposited in an open sea whose floor was upwarped before the deposition of the Ludlow Bone Bed. The Downton Castle Sandstone was laid down in shallow marine waters as beaches and shoals spread over the area. Temeside Shales reflect an area of intertidal flats and shoals close to shore and the Lower Red Downton Group indicates intertidal and estuarine sedimentation. The Holdgate Sandstone was produced by rivers spreading over marginal sediments, a fresh water environment. The Upper Red Downton Group implies brackish, turbid water under intertidal and subtidal conditions near the mouths of large rivers. Dittonian deposition was fluviatile on non-marine floodplains. The microfossil studies by Richardson and Lister (1969) over the same area show only 1% plant spores but abundant acritarchs, chitinozoa and scolecodonts in the Ludlovian. In successively younger strata the percentage of plant spores increases and the animals decrease and disappear. Close to shore, and in fresh water deposits, the acritarchs and chitinozoa are absent. The spores therefore may have come from plants living on the land. Lang (1937) arrived at the same conclusion when he found the vascular plant *Cooksonia* constantly associated with nematophytaleans, the alga *Pachytheca*, and the enigmatic *Parka* throughout the Downtonian. The association (flora) was constant whether collected in marine or in continental facies. The vascular tissue, cuticle, and cutinized spores all imply land plants. The state of preservation of *Cooksonia* (many cells preserved) and its occurrence, often in considerable abundance, imply deposition fairly near its site of growth. Perhaps therefore the Downtonian plants grew on tidal flats and flood plains whence they were readily washed into marine, brackish, or fresh water or even buried near their original habitat.

(*b*) Bohemia. Obrhel (1968) made an extensive stratigraphic and ecologic analysis of Silurian-Devonian plant life in central Bohemia. Throughout Wenlock and Budnany time algae, including codiacean green algae, were abundant. In late Budnany (Pridoli) the first vascular plants appear. The algae include those characteristic of shoals, and others that indicate somewhat deeper water. The shoals may have existed close to a volcanic island or islands which Horný (1962) postulated were produced during Ludlow time. It is possible that the first land plants, from both basal and uppermost Pridoli strata, grew on low-lying volcanic soils adjacent to a basin over which muds and limes were being spread.

(*c*) Podolia. Ishchenko (1969) reported simple vascular plants from the Rashkov beds in Podolia. They were *Cooksonia pertoni*, *C. hemisphaerica*, *C.* sp., *Rhynia major* and *Baragwanathia longifolia* accompanied by various algae. Ishchenko (Tables 1, 3) treats the Isakov as equivalent to the Ludlovian in Britain and the Rashkov and Dzwinogorod as equivalent to the Downtonian (Pridoli). Nikiforova and Predtechenskij (1968) consider the Rashkov to be Ludlovian as well. Despite the stratigraphic uncertainty, this

TABLE 3. The Skala beds of Podolia and their terrestrial flora. The Isakov is considered equivalent to the Ludlow, the Rashkov and Dzwinogorod to the Downtonian. From Ishchenko 1969; but the fossil referred to as *Baragwanathia* has now been transferred by Ischchenko to *Saxonia* Roselt, a genus of unknown affinity, which cannot be used as evidence of Late Silurian lycopods.

Skala				
	Dzwinogorod			
	Rashkov	upper		
		middle	upper	*Cooksonia*, *Rhynia*, *Baragwanathia*, *algae*
			middle	
			lower	
		lower		
	Isakov			

seems to be still another occurrence of early land plants at approximately the same point in time as in Wales and Bohemia. Prior to an examination of the material, I would doubt the identification of *Baragwanathia* which elsewhere is a Siegenian-Emsian plant of considerable size. I doubt also the wisdom of using the name *Rhynia* for a compression specimen that lacks any of the cellular details known for *Rhynia*. However the fossil may well be a naked-stemmed plant with terminal sporangia (see note in explanation of Table 3).

Like Obrhel, Ishchenko was concerned with the environment of deposition of the flora. She described Podolia, following the Caledonian orogeny, as covered by an extensive, flat-bottomed, shallow sea. To the northwest and southwest an elevated platform supplied carbonates to the sea. The resulting Skala beds consisted of limestones, dolomites, dolomitic marls, and argillites and contained a marine flora and fauna, together with the terrestrial plants that were carried in to the shallow waters. Ishchenko pictures the terrestrial plants as living on low-lying land masses on the fringe of the shallow Podolian sea. Fluctuations of the sea bottom and flooding by rivers and the seas probably caused frequent changes in the habitats of the land plants. The occurrence among the algae of siphonalean green forms led Ishchenko to the conclusion that the littoral zone of an extensive continent had a warm tropical or sub-tropical climate.

(*d*) New York. *Cooksonia* occurs in the Fiddlers Green member of the Bertie Formation of the Late Silurian Cayugan Series (Rickard 1962) in central New York State (Table 4). Goldring (in Ruedemann 1925) earlier described *Hostimella silurica* from slightly younger dolomites in western New York. Unfortunately the evidence that it was a vascular plant is not particularly convincing. It does serve to indicate that the possibility of finding land plants in the Bertie is not a new idea. Ruedemann (1925) also described the remains of some algae which he regarded as reds and browns in the Bertie. In Plate 65, figs. 3–5 are illustrated two additional putative vascular plants and one probable alga from the Fiddlers Green member of the Bertie.

The Bertie consists of drab, fine-grained argillaceous dolomites and is well known for its eurypterid fauna. Other invertebrates found in the Bertie were listed in Ruedemann (1925) and earlier papers. O'Connell (1916) argued that the Bertie was a flood-plain or upper delta deposit or that it may have accumulated as a playa lake deposit. Ruedemann (1925) on the other hand insisted that the Bertie was laid down in shallow lagoons protected from the open sea by coral reefs. Alling (1928) suspected that the Bertie sediments were carried slowly by rivers across flat-lying lands, thence into a very

TABLE 4. Position of the Bertie in New York. From Berdan *et al.* 1969.

Devonian (Gedinnian only)	New Scotland ls. Kalkberg ls. Coeymans ls. Manlius ls.	
Silurian (part)	Rondout dolo.	
	Cobleskills	
	Bertie dolo.	Oxbow Forge Hollow Fiddlers Green
	Salina Group	

salty, shallow sea. More recently Laporte (1967) has studied carbonate deposition in the somewhat similar Manlius Formation (Lower Devonian). Walker and Laporte (1970) have compared the environment of deposition of the Manlius and the Ordovician Black River Group. They recognize several carbonate facies that indicate major environments. In the absence of a detailed study of the Bertie using their approach, it may be suggested that the Bertie corresponds to the facies they call supratidal mudflats. Bertie may have been a time of extensive land with low relief, not much above mean sea level. The mudflats would have been subjected to periodic flooding, drying out, and covering by algal mats. They may have been far enough from shore to receive considerable fresh water and near enough to shore to receive salt water flooding from time to time.

(*e*) Conclusions. Present knowledge points to the deposition of Late Silurian *Cooksonia*-bearing strata at four widely separated localities in fluviatile estuarine, or lagoonal environments close to the margin of a low-lying continental area. In Wales the colonial alga *Pachytheca*, the enigmatic *Parka* (which might have grown on wet mud and produced air-borne spores) and members of the Nematophytales are found associated with *Cooksonia* in both marine and continental strata. Nematophytales possessing cuticle appear to be plants that could survive on land and Lang so considered them. Vascular tissue, stomates, epidermis, cuticle, and cutinized spores all indicate that early land plants (*Cooksonia*, *Zosterophyllum*) grew on land and not in the water. The classical reconstruction of *Zosterophyllum* as an aquatic plant is based on the preservation of many specimens as flat, carbonized compressions. Petrified specimens prove beyond all doubt that the living plant had terete stems (see Edwards 1969) with all the tissues associated with life on land. If *Cooksonia* and associates grew on fluviatile areas close to shore or on tidal flats, they could have been preserved in the state of preservation and in the facies in which they are now found fossilized.

The preservation of the specimens of *Cooksonia* that I have seen and collected indicates that the plants were not carried far from their original site of growth.

Zosterophyllum could be interpreted as favouring growth in wet mud or sand and as a plant that might survive even under conditions in which salty or brackish water was frequent. The first results from the location of its stomates as described by Lele and Walton (1961). They found stomates to be absent from the basal tuft-like mass of branches and present on the upper, presumably aerial, part of the plant. They speculated that these tufts could easily be washed out of place by either fresh or brackish water flooding over the area. That *Zosterophyllum* might survive saline conditions is indicated by its wide outer cortex composed of thick-walled hypodermal cells. As mentioned earlier such cells are found in a number of early genera and are often found today in plants growing under xerophytic conditions. Halophytic plants often show xerophytic modifications.

One can only hope that knowledge of the earliest land plant will soon rise above these highly tentative hypotheses. The growth of palaeoenvironmental studies and the increased attention being paid by plant and animal palaeontologists to the interrelation between them bode well for the future.

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